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Rhizosphere biodiversity as a premise for application in bio-economy

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ABSTRACT

Use of fossil fuel and its products have led to environmental pollution, greenhouse gases emissions, global warming and climate change. In order to mitigate and eradicate these problems, bioeconomy was conceptualized. Bioeconomy is deviation from dependence on fossil fuel to a situation where biomass will not only provide food but also raw materials for the industry including provision of bio-diesel. The major debate about bioeconomy is its sustainability. Sustainable bioeconomy should involve highly developed understanding of genetic materials and cellular reactions to redesign and produce novel methodologies and products. It is suggested that sustainable production system among other factors must minimize the excessive utilization of external resources. It should exploit natural mechanisms like nutrient cycling and release, fixation of nitrogen by bacteria and biocontrol mechanisms. Biomass is required in such magnitude such that sustainable intensification should be the watch word. In dealing with sustainable intensification, soil fertility is a major factor to be considered. In the past, management of soil fertility centered on use of inorganic fertilizers but this has not been sustainable. Use of both living and dead organic matter has been suggested as the means to sustain soil fertility. Living organic matter especially the plant-mediated organisms are known to be high in rhizosphere. Technological innovation in rhizosphere biodiversity is believed to bring about the next green revolution in agriculture. Soil fertility and productivity are enhanced by several soil inhabiting microorganisms such as rhizobia, mycorrhiza, yet maximum crop yield has not been achieved. The exploration, management and manipulation of these rhizosphere organisms are vital to maximizing crop yield. Multifaceted use of inoculum with both biofertilizers and biocontrol abilities are now areas of ongoing research. Specific yield target and site specific multifaceted multi-inoculum production should be the new research strategy.

1. Introduction

Bioeconomy is a teeming terminology in the frontier for green and low or carbon free economy. The shift from dependence on fossil fuel has placed a challenge to develop bio-based economy. In such economy, agriculture will provide quality food for the growing population in addition to raw materials for industries and energy. Such bio-based economies should ensure reduction of greenhouse gases in transiting to the system (Huisingh et al., 2015; Pülzl et al., 2014). It is noted that bioeconomy depends on sustainable agricultural production and utilization of these produce for human and animal consumption and renewal raw materials for industries and fuel (Ingrao et al., 2016). Such sectors that produce and use the produce like agriculture, horticulture, fisheries, forestry, bioenergy and biorefineries should be involved (Koukios, 2015; Lopes, 2015).

At the heart of bioeconomy is biomass production which is the building block for such economy. Without sustainable biomass production, the whole story about bio-based economy will be a mirage. The core in bioeconomy is the continued sustainable production of food and fiber, which is a key priority in fostering innovation for producing quality biomass. It is envisaged that innovations in soil biological fertility are able to sustainably provide future requirement for food stuff, feed, fiber and biofuel (Hatfield and Walthall, 2015). A large proportion of diverse organisms within terrestrial ecosystems are found below ground in soils. And they play a lot of roles in ecosystem services. In plant ecosystem, rhizosphere is a zone with rich microbial composition (Prashar et al., 2014). All aspects of agricultural practices require a better understanding of rhizosphere processes that facilitate plant growth and disease suppression. Therefore studying the intricate relationship between crop, soil and microbes in the rhizosphere is integral for sustaining healthy and high yielding production systems

Rhizosphere diversity is therefore a term to decipher the numerous organisms inhabiting the soil, closest and mostly influenced by plant roots. Plants grow in intimate association with complex

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microorganisms especially within the rhizosphere. Rhizosphere is intersecting of soil, plant and microorganisms and a niche for high microbial activities (Huang et al., 2014; Nicolitch et al., 2016). Hence, it's vital to study microbes in close proximity to plants as a way to elucidate their functions in the environment. Microorganisms that establish symbiotic interactions with plants play significant role in agricultural productivity and thus have potential for application in sustainable production. It is also predicted that the advancement in microbial techniques will lead to the new green revolution. Firstly, this review papered to give dissects of bioeconomy and the significance of soil management in sustainable biomass production. It further enumerates on the role rhizosphere biodiversity plays in fostering sustainable biomass production and the organisms involved in accomplishing these functions. Additionally, this article suggests how inoculum production can be managed and fostered for more efficient biofertilization. It is also observed that there should be site and yield-targeted specific inoculum production. Such inoculum will be a consortium of different organisms for different purposes with the sole aim of achieving specific yield and abundant biomass level. The paper is concluded by reviewing several literatures on biotechnological advancements in rhizosphere diversity.

2. Dissect of bioeconomy; the green economy

In the emerging and challenging global issues of food insecurity, climate alteration, natural resource sustainability and high dependence on manufactured resources, bioeconomy is noted as means to tackle them (Ollikainen, 2014; Staffas et al., 2013).The urgent need to reduce greenhouse gases emission which leads to climate alteration is the major factor driving the interest in bioeconomy (Pätäri et al., 2016). Dependence on fossil fuels for energy generates a lot of these greenhouse gases (Scheiterle et al., 2017). Use of fossil fuel is noted as the major source of CO_2 emission, its burning also generates N_2O (UEPA, 2017). It elaborated that human use of petroleum for light, heat, and movement in the United States constitute the highest greenhouse gas emissions (39%), excluding its use for industries, agriculture and other energy related issues (Fig. 1). So there is need to deviate from their use. More so, another motivating factor in bioeconomy is swift biotechnological advancement in biological sciences, with unique biological products (Global Bioeconomy Summit, 2015).

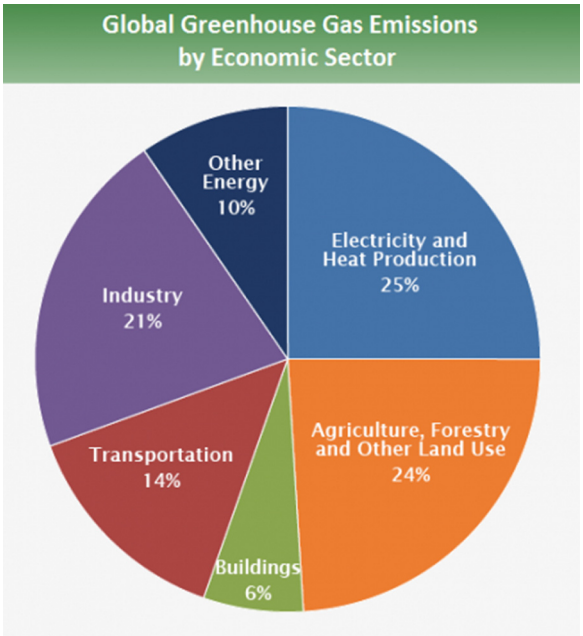

Fig. 1. Global greenhouse emission by economic sector in US. Source: (IPCC, 2014).

So what is bioeconomy? Bioeconomy is defined by European Commission (2012) as an economy using animal and plant resources and their wastes from land and water bodies as raw materials for industry and power generation. In addition, biologically based initiatives to such industries are included (Loiseau et al., 2016). Bioeconomy as a concept according to McCormick and Kautto (2013) has its building blocks derivable from renewable plant and animal resources. Such economy unites the reusable and non-synthetic biological resources with biological mediated processes (Scarlat et al., 2015). The peculiarity in all the definitions is biological resource or biomass as the input in bioeconomy.

Consequently, bioeconomy covers the fields of agriculture related industries including those that use renewable materials as their primary input (Ollikainen, 2014). Furthermore, natural techniques and materials from renewable sources are used in medicine, diagnosis, production of nutrient rich crops, power, chemicals, and materials, for wealth creation and reduction in environmental degradation (Pellerin and Taylor, 2008). As a consequence, bioeconomy will require firstly consistent availability of cheap mechanism for supply of feed stock, which is biomass.

The debate on biobased economy is majorly on its sustainability. The capacity of such a system to sustainably produce food and at the same time produce biomass for the industries and biofuel is very questionable. Moreover, introduction of new crop variety could possibly compete with the available land for food production. And these new crops could introduce new pathogens and pests that may constitute a problem for the food crop species. As a sequel, according to McCormick and Kautto (2013) sustainable bioeconomy should involve highly developed understanding of genetic materials and cellular reactions to redesign and produce novel methodologies and products. Secondly, it should entail the use of renewable biological material and capable biological processes to sustain productivity. Lastly it is suggested that biotechnological knowledge and applications should be integrated across a range of sectors. A bioeconomy entails the use of biotechnology on a large scale.

However, the overall purpose of bioeconomy is transition from petroleum to a total dependence on biomass for food and industry. It also emphasizes biological processes as mediators for bioproducts such as bioethanol, biofuel and other products. The sustainable production and utilization of biological resources should permit more production of crops from the little available resources. And at the same time limit negative impacts on the environment. This will reduce much dependency on petroleum thereby extenuating shift in climate (European Commission, 2012). Accordingly, the sustainable production and exploitation of natural resources contributes to food security, sustainable management of land resource, plummeting dependence on synthetic materials, extenuating and adaptations to alterations in climate, jobs creation and maintenance of competitiveness.

3. Sustainable biomass production

Sustainability is an all evasive term that deals with management systems that will guarantee present and future production. Sustainable agricultural production has been recognized as the solution to myriad of problems facing the globe. These problems include inappropriate use of agro-chemicals and agro-facilities, climate change and global warming. There is real need for innovations in sustainable agricultural management systems. The need for agriculture to generate additional food devoid of environmental deterioration calls for more stringent sustainability mechanisms (Milder et al., 2015; Snapp et al., 2010). The concept of sustainable development tries to reconcile profitability and human development with the working of the natural environment. It is also defined as the production of food and raw materials using techniques that lead to environmental protection. Such system conserves human health and communities and maintains animal wellbeing. It is production of healthy food without comprising future generation. More

so, sustainable production relies on natural, culturable and biological controls.

In Pretty et al. (2011), sustainable production systems should showcase the following key attributes namely:

1 use planting material and breeds with a low input demand;
2 minimize the excessive utilization of external resources;
3 exploit natural mechanisms like nutrient cycling and release, nitrogen fixation by microbes and biocontrol mechanisms;
4 reduce applications with negative influence on the surroundings and community health;
5 judicious use of human resources in adaptations and innovations and resolution of social problems; and
6 Minimize management systems that impact negatively on the environment.

Farming systems displaying such attributes are distinct from conventional systems. It is believed that agricultural sustainability programs result in changes in agricultural production inputs (e.g. use of plant growth promoting rhizobacteria (PGPR) in place of inorganic inputs; pesticides to biocontrol; from ploughing to minimal soil disturbance). With higher demand for biomass production, it is suggested that a better concept should be sustainable intensification (Tilman et al., 2011). Mueller et al. (2012) suggests that sustainable intensification of agricultural production will require considerable changes in nutrient and water management in the soil. Therefore, soil resource management is a key to sustainable intensification.

3.1. Soil management: the sustainability intensification issue

Recently, the rate of degradation of soils worldwide has led to intensified effort on the security of soils. Thus emphasizing the vital role soil plays in ecosystem services (Dobbie et al., 2011; European Commission, 2012; Robinson et al., 2013; Wall and Bardgett, 2012). Soils are basic in the shift to a stable bioeconomy. A major concern in sustainability for biomass production should rest significantly on management of soil resource. Knowing that soils are non-renewable resource and globally provides 95% of food directly or indirectly (FAO, 2017). This means that biomass production depends on soil quality, and continuous biomass production on soil's sustainability. So far, there is insufficient knowledge on sustainable management of soils within a bioeconomy (FAO, 2017) yet it is very important to ensure sustainable use of soil resources (Montanarella and Vargas, 2012).

Any lapse in the proper management of soil leads to catastrophic issues either in the short or long run. For example, diminishing soil quality threatens food security, leads to climate alteration and ecological deterioration (McBratney et al., 2014). Soil health is diminished through erosion, soil carbon (C) and nutrients loss. Cultivated soils generally lead to loss of 25–75 % of the native soil C ((Lal, 2014). More so, agricultural intensification increased soil nutrient mining during crop production. Nutrient requirement of crops were met through inorganic fertilizers with detrimental environmental and public health cost (Jones et al., 2013). Use of nitrogen (N), phosphorus (P) and potassium (K) fertilizers supplemented some nutrients removed by intensive cultivation. Yet many mineral nutrients are improperly replenished, thus resulting to negative soil health and nutritional imbalance (Jones et al., 2013).

Summary of reviews by Garnett and Godfray (2012) and Buckwell et al. (2014) on sustainable intensification, showcases increase nutrient use efficiency, improve biodiversity and functioning of the ecosystem while increasing productivity Guidelines for sustainable soil management according to FAO (2017) also emphasizes increase in biodiversity and organic matter among other factors. Addition of organic materials is crucial in increasing biodiversity and organic matter and the overall functioning of the soil. More so, according to Hatfield and Walthall (2015) improved soil biological activity is suggested as a means of increasing the productive capacity of the soil. New technologies that advance nutrient availability and the effectiveness of soil biological fertilizers have the possibility to restore degraded soils and improve their capacity for production and feeding the world's population. Rhizosphere being the soil area with higher diversity, functionality and content of soil organisms holds a lot of hope (Huang et al., 2014).

3.2. Rhizosphere diversity; a tool for the new green revolution

Microorganisms are important drivers in the functioning of ecosystem and its sustainability. The diversity of organisms dwelling in soils is extremely huge, and their roles are likewise diverse (Dighton and Krumins, 2014).The recent demand for sustainable and increased crop yield has reinvigorated the study of soil inhabiting microbes. Rhizosphere is soil zone rich in plant interacting microorganisms. It is worthy of note that advances in the rhizosphere has led to milestones in agriculture, environmental remediation, water infiltration, medical discoveries, industrial application and many other fields (Hill, 2012). And it is hoped that the next green revolution will be achieved by advances in biological fertility. The rhizosphere is an important niche area sustaining the interchange of materials between plants and their inclusive soil surroundings. Many organisms are involved in this exchange resulting in myriads of interactions among plants and their promoting and pathogenic microbes both in the soil and in the plant (Hou and Oluranti, 2013; Igiehon and Babalola, 2017).

The most popular definition is that rhizosphere is the soil closest to and highly influenced by plant root (Nicolitch et al., 2016; Pascual et al., 2016) while Lynch and Whipps (1990) stated that rhizosphere is not just the thin soil layer bordering the root but comprises of three main zones. The root cortical with the rhizoplane known as the endorhizosphere; the rhizoplane encompasses the root epidermis and associated mucilage while soil closest to the root is ectorhizosphere.

The root, soil and the microbes are in continuous interaction and each influences the existence and performance of the other. Plant exudates which are food for the microorganisms, determine the type of organisms that could survive in the rhizosphere; the soil also influences the plant and the microbial survival. In addition, microorganisms determine fertility of the soil thus influence plant performance. According to Chaparro et al. (2014), it is now known that plant engineers the organisms in their immediate soil surroundings. Plants from their origins are known to change the microbial abundance at the rhizosphere. Therefore, plant species support unique microbial population. The resultant microbiome is a product of the differences in type of root exudates (Bais et al., 2006; Rasmann and Turlings, 2016) and rates of uptake of nutrients by plants (Bell et al., 2015). Root exudates in turn are determinant factor of the genetic variability of the crop (Aira et al., 2010; Bouffaud et al., 2012).

In the past, plant breeding and microbial studies were carried as separate entities but in recent time the close association of plants and microorganisms are seen as unified ecological niche known as a holobiont (Vandenkoornhuyse et al., 2015). Given the interdependence of plants and rhizosphere microbes (Berendsen et al., 2012; Mueller and Sachs, 2015), leads to a logical proposition. Variations in genetic and phenotype plant traits that sustain microbiome which are beneficial to plants deserve a fitness advantage. Thus, the ability of plant to sustain beneficial microbiome is a trait that should be selected in plant breeding. The benefits derivable from the microbiome must supersede the carbon and energy gotten from the plant. It is believed that the holobiont may have been the unit under selection, guiding evolution towards plant traits that supported favorable microbiome. This is a new area of research. On the other way, a holistic and mechanistic study of the interactions is very pertinent and could be the long awaited miracle to the new green revolution. The entire microbial community involved in enhancement of growth and development of specific plant genotype in a specific environment under certain management conditions should be studied and engineered for maximal sustainable yield increase. Such

that inoculum production should no longer be a strain of one beneficial organism but a consortium of biological agents specific to each or groups of plant genotype under certain environmental condition. New area for research should be on site specific microbial inoculum production that should address the soil specific problems, which could include nutrient deficiencies and fixations, environmental hazards and adaptations and pathogenic resistance. Such microbial consortium should be adaptable to coexist within the rhizosphere.

3.3. Mechanisms for soil fertility and productivity enhancement by rhizosphere microorganisms

Soil fertility has to do with nutrient availability in the soil while productivity deals with all other factors of production including adaptability to variability in climate (drought, heat), pathogen and pest resistance and even nutrient availability and uptake efficiency.

3.3.1. Soil nutrients as mediated by microorganisms

The use of rhizosphere organisms in soil fertility management is well established thus involving several mechanisms to bring about plant growth enhancement. The first and foremost is nutrient cycling and release, without which life will not continue to exist. These resources are finite so without their recycling, it's impossible to reuse them. Both organic and inorganic nutrient materials are converted by these organisms to forms that can be used by plants. Almost all organisms, both macro and micro-organisms are involved in decomposition, depending on the type of substrate added. Furthermore, these organisms enhance nutrient use efficiency of plants. Mycorrhizae and plant growth promoting rhizobacteria (PGPR) are among the highly researched organisms that mediate plant growth. Table 1 shows names of different organisms and the nutrients they facilitate for crop use. As the name is, PGPR are those bacteria that inhabit the rhizosphere and benefit plant in a number of ways. According to Bishnoi (2015), the use of bacteria to boost plant growth in agriculture is dated to over one million years, and using bacteria to sustain agricultural productivity is not new.

As a matter of fact, the most widely recognized and researched mechanism for increasing soil fertility by microbes is nitrogen fixation by rhizobia. Some rhizobia are free living while others live in the roots of leguminous plants. Rhizobia are usually associated with legumes symbiotically in which nitrogen-fixing nodules are formed (Antoun and Prévost, 2005). In particular, *Rhizobium spp*. is actually soil borne and is known for promoting plant growth through nitrogen fixation. According to Avis et al. (2008) these bacteria synthesize plant growth hormones and can make organic and inorganic phosphates soluble.

In relation to rice production, biological N fixation (BNF) reduces inorganic N fertilizer use, thus minimizing environmental problems associated with the use of urea. In upland rice cultivation (Choudhury et al., 2014), aerobic bacteria *Azotobacter* inhabit the aerated rhizosphere and fix atmospheric N. Anaerobes like *Clostridium* live in part of the soil with less oxygen and fix N. In lowland rice cultivation, the favorable organism for such ecosystem is *Azolla* and cyanobacteria. *Azolla* can fix huge amount of N in symbiosis with *Anabaena* while the blue-green algae can fix atmospheric N as a free-living aquatic organism Other organisms that fix nitrogen in rice environment are *Azospirillum*, *Herbaspirillum*, and *Burkholderia* (Baldani et al., 2000).

Another very important mechanism in soil fertility management using microbes is P solubilization. Phosphorus in soils is highly immobile because they are easily fixed and unavailable for plant use. Both bacteria and fungi are implicated as P solubilizing microorganisms (PSM). These organisms produce organic acids, protons or phosphatase enzyme that mineralizes organic P. The genera and species that are PSM have been described by (Babana and Antoun, 2006). These include *Rhizopus spp*., *Penicillium rugulosum*, *Aspergillus awamori* and *Penicillium chrysogenum* (Babana and Antoun, 2006). Other genera known for PO_4 solubilization are Burkholderia, Cedecea, Cronobacter, Enterobacter, Pantoea and Pseudomonas (Ambrosini et al., 2012; de Souza et al., 2013) while Chen et al. (2006) identified several strains belonging to genera Bacillus, Rhodococcus, Arthrobacter, Servatia, Chryseo, Gordonia, Phyllobacterium and Delftia as PO_4 solubilizer. Mycorrhizae are widely known for making P available for associated plants especially in P deficient soils.

In addition, several species of rhizobia are able to solubilize phosphates (Miransari, 2013). Such groups like *Rhizobium, Bradyrhizobium, Mesorhizobium and Sinorhizobium*, in addition to N fixation are known for production of growth regulators and inorganic phosphate solubilization (Hayat et al., 2010). They are also known for disease suppression (Siddiqui et al., 2007). Solubility of micronutrients such as iron, manganese and zinc are improved by soil microbes through several mechanisms (Miransari, 2013). Very importantly also, in high concentrations of soil microelements, soil microorganisms do reduce their toxicity on plant and on the surrounding by various mechanisms (Miransari, 2013).

3.3.2. Soil productivity and microbial intervention

Soil productivity is the ability of the soil to produce high yield. As shown in Table 2, microbes directly enhance the growth of plants through production of phytohormones. Such substances or hormones (gibberellins, auxins, IAA, etc.) confer direct growth promotion on associated plants (Compant et al., 2010). Other productivity factors mediated by microbes include adaptability and tolerance to

Table 1
Different Microbial inocula for soil fertility improvement.

Factor of fertility involved	Microbes involved	Reference
N fixation	*Rhizobium, Mesorhizobium, Bradyrhizobium, and Sinorhizobium*	Antoun and Prévost (2005),
a symbiotic	*Azotobacter, Clostridium, Azolla, Azospirillum, Herbaspirillum, and Burkholderia, blue-green algae,*	Mian (2002)
b non symbiotic	*Acetobacter, Azoarcus spp., cyanobacteria, Bacillus spp., Enterobacter spp., Xanthobacter spp., Gluconacetobacter diazotrophicus, Achromobacter spp., Arthrobacter spp., Azomonas spp., Clostridium spp., Beijerinckia spp., Corynebacterium spp., Rhodospirillum spp., Klebsiella, spp., Derxia, spp., Herbaspirillum spp., Pseudomonas spp., Rhodopseudomonas spp*	Hashem (2001) Baldani et al. (2000) Miransari (2013)
Phosphate solubilization	*Paenibacillus, Pseudomonas, Aspergillus, Penicillium), Rhizobium, Bradyrhizobium, Mesorhizobium, Sinorhizobium andMycorrhizae,*	Babana and Antoun (2006) Hayat et al. (2010)
K solubilization	*Paenibacillus mucilaginosus, Bacillus mucilaginosus, Bacillus circulans*	Li et al. (2007) Liu et al. (2012) Zeng et al. (2012)
S oxidation	*Thiobacillus, Thiothrix, Chlorobiaceae, Beggiatoa, Chromatiaceae, Ectothiorhodospiraceae*	Meyer et al. (2007)
Micronutrient solubilization	Mycorrhizae	Jin et al. (2010) Marschner et al. (2011) Podile and Kishore (2007), Selosse et al. (2007)
Heavy metal remediation	*Bacillus* spp., *Pseudomonas* spp., *Azotobacter* sp., *Enterobacter* spp., and *Rhizobium* spp.	Zhuang et al. (2007) Matilla et al. (2011).

Table 2
Soil Microbes for overall productivity enhancement.

Factor of productivity	Microorganisms involved	References
Growth hormones	*Pseudomonas spp., Enterobacter sakazakii* and *Klebsiella oxytoca*	Compant et al. (2010)
Biocontrol	*Mycorrhizae, Rhizobium spp., Bacillus, Pseudomonas spp., Enterobacter sakazakii* and *Klebsiella oxytoca*	Liu et al. (2007), Nasrin and Rahman (2007) Yuttavanichakul et al. (2012)
Adaptation to drought/ increased water uptake	Mycorrhiza	Selosse et al. (2007)

environmental stress like drought, toxic compounds or pollutants and resistance to pests and pathogens (biocontrol). According to Innerebner et al. (2011) plant-associated microbes protect plants against pathogens. Bacillus is known as biocontrol agent. According to Nasrin and Rahman (2007) PGPR live close to the roots while depending on root exudates, profit the plants by changing the nutrient solubility and availability and produce antibiotics around the roots to ward off pathogens. Further to Rhizobium spp. growth promoting effects, they are highly known for suppressing disease (Siddiqui et al., 2007). Another mechanism for biocontrol by *Rhizobium spp*. is that they produce iron-chelating siderophores. These siderophores would capsulate and thereby reduce the availability of iron to other microorganisms within the environ (Avis et al., 2008). Yuttavanichakul et al. (2012) investigated the use of *Bradyrhizobium* and some soil isolated PGPR in biocontrol of peanut *Aspergillus niger*. They found out that all isolates of PGPR could produce auxins which led to increase in peanut yield while 11 of the PGPR isolates inhibited growth of fungus *A. niger*. Furthermore, when some isolates that weren't effective in controlling the disease were co-inoculated with *Bradyrhizobium* spp., the root rot disease was controlled. They also found out that when rhizobia were inoculated with some selected PGPR, N fixation was increased and use of fungicide was reduced, thus providing appropriate approach for sustainable agriculture. According to de Salamone et al. (2012) inoculating *Pseudomonas fluorescens* and *Azospirillum brasilense* on 3 genotypes of rice led to increase in biomass and grain yield of the cultivars over the control.

More so, arbuscular mycorrhiza (AM) fungus has biocontrol ability (Avis et al., 2008). Whipps (2004) in his review on potentials of mycorrhiza in biocontrol of plant diseases mentioned specifically the Glomus spp. Generally, symbiotic association with Glomus spp. controlled disease in numerous root plant pathogens. Glomus spp. reduced disease *Alternaria solani; G. intraradices* decreased *Xanthomonas campestris* in alfalfa plant (Liu et al., 2007). Therefore *Glomus spp*. can be used in biocontrol of plant diseases. The likely mechanism of *Glomus spp*. in biocontrol of both root and foliar pathogens are (i) growth inhibition of pathogen by the AM fungi waste, (ii) competitive edge for nutrients (fungal hyphae allow plant access to greater soil volume), (iii) better nutrition for the plant (mycorrhiza colonization increases nutrient solubilization and absorption in plants), (iv) change in plant root architecture, etc (Avis et al., 2008).

3.3.3. Biochemical mechanisms of PGPR for soil fertility and productivity enhancement

Mechanisms for the action of PGPR largely depend on either production of hormones, antibiotics and/or enzymes. In symbiotic N fixation, nodule formation is a prerequisite. Production of indole acetic acid (IAA) is essential in developing symbiosis and in nodule formation. Remans et al. (2008) found that co-inoculation of beans with *Azospirillum brasilense* Sp 245 and Rhizobium etli CNPAF512 yield a greater number of nodules than inoculation with the mutant strain of Azospirillum that produced only 10% of IAA. Microbes containing IAA are essential in promoting growth and development in plants (Akbari et al., 2007; Baudoin et al., 2010; Spaepen et al., 2008) and in establishing plant-microbe interaction (Spaepen et al., 2008). Nitrogenase is the enzyme responsible for nitrogen fixation and it's usually inhibited in the presence of oxygen. Rhizobia in the root nodules of legumes moderate oxygen levels in the roots thereby enhancing the performance of nitrogenase enzyme for N fixation (Dixon and Kahn, 2004). All diazotrophic microbes that fix N have been found to contain nitrogenase in spite of their different morphology and environmental differences. The gene responsible for the synthesis and functioning of nitrogenase is known as nif genes (Boucher et al., 2003).

Phosphate (PO_4) solubilization is another way PGPR improve plant growth. Such bacteria do so through production of organic acids, siderophores or hydroxyl ions (Sharma et al., 2013). Another mechanism for PO_4 solubilization according to is through rhizosphere acidification. Richardson et al. (2011) and (Richardson and Simpson, 2011) reported production of enzymes such as phytase and phosphatase for solubilization of phytate (which is organic form of phosphorus) and other phosphates.

In phytopathogenesis, some PGPR produce hydrogen cyanide (HCN) and/or enzymes that degrade fungal wall such as chitinase. Another mechanism in pathogenesis is production of siderophores, which chelate iron in iron limiting soil condition. And bacteria associated with plants largely produce them (Ambrosini et al., 2012; de Souza et al., 2013). Bacteria producing siderophores are able to compete better than other microbes for colonization of plant tissues, thereby excluding other microbes including disease causing ones from the ecological niche (Loaces et al., 2011). Maize siderophores production by Bacillus was very effective against the growth of Fusarium spp and other pathogens (Szilagyi-Zecchin et al., 2015; Tortora et al., 2011) Siderophore production by PGPR makes iron available for plant uptake. According to Dimkpa et al. (2009), plants unlike pathogens are able to utilize iron siderophores complexes.

Adaptations for growth enhancement under stress condition is through production of 1 amincyclopropane 1 carboxylate (ACC) deaminase enzyme by bacteria inhabiting rhizosphere of plants. Ethylene at low concentrations promotes plant growth but in stress conditions, ethylene becomes so high thereby being detrimental to plant growth. ACC deaminase enzyme produced by bacteria reduces ethylene concentration during biotic or abiotic stress (Ali et al., 2014; Glick, 2005). ACC is produced by plant roots and is a precursor to ethylene production. In stress condition, microbes produce ACC deaminase which metabolize ACC for the microbes to utilize them as nitrogen source (Glick, 2005), thereby preventing production of ethylene. Other mechanism for direct growth promotion involves production of auxins, cytokinnins, gibberellins and abscisic acid.

3.4. Management of the rhizosphere microbes for effectiveness in biomass production

In order to manage soil sustainably, Powlson et al. (2011) emphasized that one of the methods is by maintaining biodiversity. As already stated, soil organisms especially the rhizosphere organisms are vital for enhancing growth and development of plants and thus in biomass production. An understanding of the basic principles, the function and diversity of rhizosphere microbial ecology, is a prerequisite for application of soil microbial technology. The first angle in use of rhizosphere organism is identification of the microbiome associated with the rhizosphere of plants and subsequent multifaceted inoculum production. The essence of adding inoculum to the soil is to bring about microorganisms that promote plant growth which by shifting from natural to managed ecosystems have been depleted. In the past, most inoculum were single microbe constitute but it had limited application. One must select the right combination of microbes, determine their inoculating potential, their ability to persist in the soil, their survival under stress, etc. (Miransari, 2013). The use of single microbial inoculum cannot

work efficiently because a set of targeted benefits to plants including nutrient addition and solubilization, disease control and environmental adaptation has to be built into production of inoculum (Artursson et al., 2006; Belimov et al., 1995; Toljander et al., 2006). Generally, single rhizobium inoculation of legume crops enhances yield by 10–20% depending upon the crop and soil conditions. *Azospirillum* enhanced the yields of pearl millet (23%), sorghum (18%) and cotton (30%). It has also been found that multi-microbial inoculum performs better in terms of biomass increase and is more cost efficient. A study was carried out in Pradesh soil which had low N and K and medium to high P, micronutrients except iron, was low to medium and biotic constraints with plant-parasitic nematodes infestation that affected root nodules (Chouhan, 2011). A comparative study was undertaken to study the effects of application of: (a) Farm yard manure (FYM) + *Rhizobium* inoculants and (b) FYM + consortium of biofertilizer that included the N_2 fixer *Rhizobium, Azotobacter* and *Azospirillum* as well as the phosphorus solubilizer (*Panebacillus*) inoculants, (c) FYM + chemical fertilizer and (d) combined effect of FYM +, consortium of biofertilizer + chemical fertilizer for lentil cultivation. The consortium proved to be highly advantageous over others. It increased the seed yield by 29.7% in the year 2010 and 30.8% in 2011. In fact, the FYM + *Rhizobium* gave 43.13 kg/ha seed yield while the consortium had 381.7 kg/ha seed yield (Table 3). More so, of all the treatments, the microbial consortium had the highest benefit cost ratio (Chouhan, 2011). Pot experiment by Maiyappan et al. (2010) with microbial consortia containing nine microbial strains (grouped under Bacillus spp., Streptomyces spp., Azotobacter spp. and Frauteria spp.) gave significant increase in root volume and shoot dry mass over the control. The result also showed that total dry mass was higher in consortia treated pots than those treated with chemical fertilizer. Bharathi et al. (2017) in field biofertigation experiment found that treatment with microbial consortium (Pseudomonas, Azospirillum and Phosphobacter) gave higher root and shoot length and dry weight of bhendi than the controls. Also microbial consortium at single application gave highest nutrient N, P and K uptake than the splits. Therefore, site or area specific multi-inocula production is thus recommended. This builds on the problems envisaged or prevalent in such agro-ecological zone. Table 4 is adaptation from Kumar and Jagadeesh (2016) showing consortia effective against different plant pathogens, the reason for choosing them and mechanism of actions.

Microbial species and strains differ in performance under varying conditions, which determines their biofertilization efficiency and their use. For example, organisms isolated under stressful conditions may perform more efficiently under stress, as compared with those isolated under optimum condition (Miransari, 2013). Effective colonization, multiplication and proliferation are very relevant for any inoculation to be effective (Kamilova et al., 2005). Colonization begins by the plant attracting the organism contained in the inoculum, followed by recognition, adherence, invasion (only endophytes and pathogens), colonization and growth, and several strategies to establish interactions. Plant roots initiate the interaction with soil microbes by signals that are recognized by the microbes. This leads to colonization (Berg, 2009). PGPR reach root surfaces by active motility facilitated by flagella and are guided by chemo-tactic responses. This implies that colonization and functioning of PGPR depend highly on their abilities to take advantage of a specific environment or to adapt to changing conditions such as plant species.

The use of microbial inoculum is engineered through two means. The first one already discussed is biofertilization or bioaugumentation, which involves introduction of new organisms through inoculation. The second is biostimulation which involves provision of nutrients to the indigenous microbial populations to support growth and increase metabolic activity required to degrade contaminants (Mandal et al., 2011). This is also important aspect in managing microbial inoculum for use in sustainable agricultural production. Examples include application of organic material to the soil which is food for the microbes or some special nutrients produced specifically for microbial' growth. The choice of inoculum carrier is also very important because this could affect the efficiency of the inoculum survival and overall performance.

Other management techniques include application of manure, plant residues, minimal tillage, maintaining of plant cover, etc.

3.5. Biotechnological advancement in rhizosphere engineering

The rhizosphere diversity could be explored using culture-dependent and independent approaches (Pascual et al., 2016). The conventional method of isolation for microbes was culturing using serial dilution and plate count method. Only about 0.1–1% of the organisms in soil can be cultured, thus making studies of the population extremely difficult (Farrar et al., 2014; Pankhurst et al., 1996). Moreover, culturing is laborious and time consuming (Zengler 2009). In spite of that, according to Vartoukian et al. (2010), culture dependent methods are still very necessary because they provide information which cannot be gotten from non-culture methods. That is it is fundamental to the physiological and genetic characterization of specific bacterial strains with functional traits. Isolation of individual bacteria species in pure cultures permits evaluation of impacts and further manipulations for the benefit of the environment (Pascual et al., 2016). As a matter of fact, culturing method complements the molecular approaches. Thus, permit further in-depth metabolic, physiological and genomic characterization and thereby the possibility to obtain a better understanding of their roles in the rhizosphere (Pascual et al., 2016).

The use of phospholipids fatty acid profiling (PLFA) and Molecular methods are major types of culture independent methods. Phospholipids fatty acid profiling gives information about the overall structure of soil microbial community (Willers et al., 2015). PLFA analysis can be applied to microbial biomass determination or used as biomarkers of community structure; and to give an overview of the role of the microbial community. It is often used in soil studies to distinguish between bacterial and fungal biomass. Fungal to bacterial (F: B) ratio can be gotten by dividing the sum of the mole percentage values of the fungal fatty acid markers (saprotrophic and mycorrhizal) by that of the

Table 3
Effect of Farmyard Manure, Chemical Fertilizer and Biofertilizer on seed yield and Economic Return of Lentil cv. DPL-62 at Agra, pooled data of two years.

Treatments	Seed Yield (Kg/ha	Increase in Seed Yield (Kg/ha)	Total Cost of Treatment (Rs./ha)	Gross Return (Rs./ha)	Net Return (Rs./ha)	Benefit Cost Ratio BCR
Control	842.91	–	14,062.63	34,116.4	20,053.77	2.30
FYM + Rhizobium	886.04	43.13	14,612.83	35,441.6	20,828.97	2.42
FYM + Rhizobium + PSB + Azospirillum	1224.61	381.7	14,712.83	48,984.4	35,271.7	3.32
FYM + Chemical Fertilizer (Urea 12.5 kg/ha; SSP 50 kg/ha)	1359.0	516.09	19,647.91	54,360.6	34,712.09	2.76
FYM + Rhizobium + PSB + Azospirillum	1416.43	573.52	19,797.88	56,657.2	36,859.12	2.86
Rhizobium + PSB + Azospirillum + Chemical fertilizer (Urea 12.5 kg/ha; SSP 50 kg/ha)						

(Adapted from Chouhan (2011)) Note: FYM - farm yard manure; PSB – phosphate solubilizing biofertilizer; SSP – single super phosphate.

Table 4
Microbial consortia effective against different plant pathogens, the reasons for choosing them and mechanism of actions.

Sl. No.	Microbial Consortium al Consortium	Reasons for choosing the microbes and pathogens against whom tested	Plants	Mechanism of action	References
1	*Trichoderma harzianum* Tr6 & *Pseudomonas sp*. Ps14	Ps14 Isolated from cucumber rhizosphere to test their combined effect against *Fusarium oxysporum* f. sp. *Radicis cucumerinum*	*Cucumis sativus*, *A. thaliana*	Primed expression of a set of defense-related genes	Alizadeh et al. (2013)
2	*Azospirillum* sp. AZ204 & *Pseudomonas fluorescens* Pf1	Selected based on prior report of AZ204 as N fixer and P solubilizer, Pf1 as BCA and tested against *Rhizoctonia bataticola*	*Gossypium hirsutum*	Plant growth promotion	Marimuthu et al. (2013)
3	*P. fluorescens* EBC5 & P. *fluorescens* EBC6	Isolated from chilli root tissues and selected based on mycelial growth inhibition of *Pythium aphanidermatum in vitro*	*Capsicum annum*	ISR	Muthukumar et al. (2010)
4	*Bacillus amyloliquefaciens*& IN937a *B. pumilus* IN937b	Prior use as mixtures provided broad spectrum of disease protection, tested against *Sclerotium rolfsii*, *Ralstoniasolanacearum*, C. *gloeosporioides*	*Capsicum annum, Solanum lycopersicum*	Increased SOD and PO activities	Jetiyanon (2007)
5	Mixture of *Pseudomonads*	Selected based on antifungal activities of the strains, tested against *Gaeumanno mycesgraminis var. tritici*	*Triticum aestivum*	Antibiosis	Duffy and Weller (1995)
6	*T. harzianum, P. fluorescens strain 2*-79RN10	Selected based on antifungal activities of the strains, tested against *Aphanomyceseuteiches f. sp. pisi*	*Pisum sativum*	Siderophore; ISR; Plant growth promotion	Dandurand and Knudsen (1993)
7	*P. aeruginosa* (PHU094), *T. harzianum* (THU0816), *Mesorhizobium sp.* (RL091	Compatibility checked beforehand of the strains BCAs and antagonistic behavior against pathogen, tested against *Sclerotiumrolfsii*	*Cicer arietinum*	Activation of phenylpropanoid pathway and lignin deposition Antioxidant mechanisms	Singh et al. (2013)
8	*Rhizobia sp*, *B. cereus* strain BS03, *P. aeruginosa* RRLJ04	Randomly selected and mixed to see the efficacy of the consortium against *Fusarium udum*	*Cajanus cajan*	Increased PAL, PO, and PPO activities	Dutta et al. (2008)
9	*B. licheniformis* MML2501, Bacillus sp. MML2551, *P. aeruginosa* MML2212, *Streptomyces fradiae* MML1042	Randomly selected based on prior knowledge of effectivity against Sunflower necrosis virus disease (SNVD)	*Helianthus annuus*	Plant growth promotion	Srinivasan and Mathivanan (2009)

Adaptation from Kumar and Jagadeesh (2016) Note: ISR – induced systemic resistance, SOD – Superoxide dismutase, PR – Pathogensis related; PO – Polyphenol oxidase, PPO – Phenylalanine and polyphenol oxidase, PAL – Phenylalanine ammonia lyase.

bacterial fatty acid markers (Frostegård and Bååth, 1996). An increase in the F: B ratio shows rise in fungal organisms in the microbial community. Variations in this ratio have been associated with environmental processes such as nutrient cycling, organic matter decomposition and carbon sequestration (Bragazza et al., 2015; Romaniuk et al., 2011) and is usually used to evaluate the effect of agricultural management systems on soil microbial communities (De Vries et al., 2006, Romaniuk et al., 2011, Zhang et al., 2012). Determination of microbial biomass in the soil using PFLA indicates microbial community structure in response to management (Zhao et al., 2014). Using fatty acids indicator for fungi, bacteria and actinomycetes describes the major microbial groups. Limitations of PLFA biomarkers include among other factor a low taxonomic resolution and inability of microbial identification on species-level. Using molecular fingerprinting techniques with fatty acid profiling could study microbial community composition to the level of species. Although several microbial taxa can be identified using whole biomarker patterns instead of single biomarkers (de Carvalho and Caramujo, 2014; Dijkman and Kromkamp, 2006), care should be taken in interpreting certain fatty acids as sole biomarkers of microbial groups.

The problem associated with the PLFA techniques is circumventing with the extraction of DNA and RNA with their subsequent analysis employing the molecular methods (Sánchez-Hidalgo et al., 2012). DNA extraction is fundamental in molecular study. Prokaryotic classifications are now based on genomic techniques (Konstantinidis and Tiedje, 2004). Classification of non-culturable bacteria using such genomic data obtained from molecular techniques, gives us understanding of microbial diversity of the plant-soil system (Konstantinidis and Tiedje, 2004). Molecular techniques using 16SrDNA gives credence to previous work based on culturing organisms from soils, but also indicate novel consortia of organisms not yet cultured. According to Muyzer and Smalla (1998). PCR amplification of 16SrDNA using primers and separation of the resultant PCR amplicons either by cloning, denaturing gradient gel electrophoresis (DGGE) or temperature gradient gels electrophoresis (TGGE) constitute the most popular molecular ecology techniques to describe bacterial ecology. Clones or bands on gradient gel can be sequence and the resultant information used to describe the diversity of the organisms in the sample. Use of these methods has contributed information on sequence-based taxonomy of soil bacteria. The clone library and multiplex amplicon pyrosequencing permit access to the prokaryotic diversity of high resolutions those resistant to in vitro culturing (Pascual et al., 2016). Recent advances in sequence technology (pyrosequencing) characterize microbial diversity of natural environments better than traditional molecular biological techniques involving cloning. According to Macrae (2000), molecular techniques classify microbial community changes at genetic level but uniformity in sampling method is the problem. This problem is now resolved by the use of small subunit ribonucleic acid (rRNA) analysis, which elucidates micro-habitats of organisms and how they interact. Type of DNA extracted from the soil gives an indication of the organisms present, though care is required as DNA can be obtained from non-viable organisms. Extraction and analysis of ribosomal RNA (rRNA) indicates the dominant active population.

Extracted DNA or RNA can be assigned taxonomic characteristics using 16S rRNA gene sequence (Sánchez-Hidalgo et al., 2012). Wegener et al. (2016) noted that such taxonomic marker gene has revealed enormous phylogenetic complexity of soil organisms. Ludwig et al. (1997) also said that another benefit of this technique in surveying bacterial diversity of soils is that a number of common taxa have been identified in different soil locations. To quantify the abundance of specific organism, approaches based on direct counting such as fluorescent in situ hybridization (FISH), real time polymerase chain reactions (qPCR) or intact polar lipids (IPLs) are used (Wegener et al., 2016). Fluorescent enables clear visualization of small numbers of cells within the host

(Farrar et al., 2014) though the basic handicap with Fluorescent method is that it is unable to isolate unculturable endophytes. The structure and function of active microbial communities can also be tracked using stable isotope probing (SIP) approaches ((el Zahar Haichar et al., 2016). They also observed that DNA and RNA SIP approaches generally give strong phylogenetic resolutions of microbes that actively assimilate root exudates. Macrae (2000) observed that molecular techniques require DNA extraction and such method require lysing and the problem with this method is ability to ensure efficient lysing and DNA recovery. He also noted that in lysing and nucleic acid recovery, large amounts of humic substances are also extracted, which contaminate the DNA thereby inhibiting subsequent molecular analysis.

Current advances in omics biotechnologies present a huge prospect to screen and analyse large and complex microbial communities and unravel and harness novel genetic resources from soil microbes (Macdonald and Singh, 2014; Ryan et al., 2009). Using metagenomics, Proteomics, metabolomics and transcriptomics, it is now possible to identify mechanisms and isolate genetic resources for maximizing nutrient cycling and nutrient use efficiency (Abhilash et al., 2012). Ryan et al. (2009) said that genomics and metagenomics have the capacity of large sequencing procedures which will enable exploration of the microbial diversity more rapidly and in greater details. Additionally, metagenomics along with traditional measures of soil physico-chemical properties could be used to determine the soil's ability to supply nutrients to crops under low input farming system, fertilizer use efficiency under conventional farming and when combined with predictive modeling, can forecast the future outbreak of disease and weeds under conservation agriculture. In poor soils, health metagenomics can be used to identify interventions required to restore the soil (Bulgarelli et al., 2012). Aguiar-Pulido et al. (2016) said that the main purpose of metagenomic is to understand the taxonomic profile of a microbial community but whole genome analysis provides hint into the functional profile of a microbial community. Functional profile is better understood using metatranscriptomic, which involves detection of genes that are expressed by the community as a whole. Using functional annotation of expressed gene, functional profile of a community can now be inferred. With metagenomics, the compositions of a microbial community under different conditions are identified. Metatranscriptomic studies elucidate the molecular differences in the composition and regulation of various processes by microbes (Eastwood et al., 2011) by providing data on community RNA (Gilbert et al., 2008). Metabolomics identifies byproducts or metabolites produced under different conditions. The metabolites released by microbial community are largely responsible for the health of the environment (Aguiar-Pulido et al., 2016). According to Glenn (2011), the advent of next generation sequencing enabled reduction of costs of large scale sequencing and increases in instrumental resolution enabled analysis of complex proteome and metabolome data (Keiblinger et al., 2012). Sequencing of RNA produces large novel sequence information, by capturing organisms or genes that couldn't be detected by DNA sequencing alone (Gilbert et al., 2008). Omic technologies have identified many new genes which have no reliably identified function (Franzosa et al., 2015).

The taxonomic identities of isolates were assigned by 16S rRNA gene sequence analysis. Electronically, there is large database of nucleotide base sequences of the small sub-unit of rRNA, 16S for prokaryotes and 18S for eukaryotes (Powlson et al., 2011). And it continues to expand exponentially. As a result, it is a means to identify organisms in soil without the need for isolation and culture. More so, there is also a rapidly increasing body of sequence data for genes encoding functions relevant to soil processes. According to Powlson et al. (2011) comparison of data with information in this growing database provides a powerful tool for identifying many soil bacteria, archaea and fungi, with varying degrees of certainty, to the genus, species or subspecies level. More precise information on which functional genes are active can be obtained from messenger RNA (mRNA), although this is technically more difficult with current methods. Methods exploiting these approaches (Hirsch et al., 2010) such as direct sequencing of nucleic acids extracted from soil and the use of microarrays could almost be regarded as a new way of classifying soils according to the range of organisms they contain, complementing traditional classifications based on particle size distribution (texture) or soil forming processes (pedogenesis). In some respects, they are likely to reveal data that is uninformative: for example, confirming known trends such as certain organisms favoring certain types of soil environment (e.g. acid or alkaline, aerobic or anaerobic). However the potential is immense

4. Conclusion

Application of rhizosphere diversity in bioeconomy is fundamental in the global shift from fossil fuel to dependence on biomass for food, fuel and raw material for industries. Sustainable biomass production rests squarely on soil resource which produces 95% of food globally. Crops depend on the soil and its composition, including its fertility and biology. Soil productivity encompasses the fertility, climatic factors and other productivity variables. Rhizosphere organisms do enhance the fertility and productivity of soils, which is recommended as a means for sustaining the soil. Microorganisms though occur naturally in the soil but their beneficial effect could be enhanced through inoculation of crops with specific microbes that are found beneficial. The premium issue in the use of rhizosphere organisms for sustainable biomass production is identifying the microbes that are associated with the crop and its environment and then proceed to inoculum production. Biotechnological advancements in rhizosphere organisms have elucidated the organisms associated with certain crops in specific soil management systems. Inoculum production should be multifaceted and should be a consortium of organisms that favors plant growth, combats pests and diseases, adapts crops to abiotic stress and increases biomass production.

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

This article does not contain any studies with human participants or animals.

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